Article:

Prescott, T.J. (2007) Forced Moves or Good Tricks in Design Space? Landmarks in the Evolution of Neural Mechanisms for Action Selection. Adaptive Behavior, 15 (1). pp. 9-31. ISSN 1059-7123

https://doi.org/10.1177/1059712306076252

Forced moves or good tricks in design space?
Landmarks in the evolution of neural mechanisms for action selection[*]

Tony J. Prescott
Adaptive Behavior Research Group,
Department of Psychology,
University of Sheffield,
Western Bank,
Sheffield, S10 2TN, UK.

t.j.prescott@sheffield.ac.uk

Abstract

This review considers some important landmarks in animal evolution, asking to what extent specialized action selection mechanisms play a role in the functional architecture of different nervous system plans, and looking for 'forced moves' or 'good tricks' (Dennett, 1995) that could possibly transfer to the design of robot control systems. A key conclusion is that while cnidarians (e.g. jellyfish) appear to have discovered some good tricks for the design of behavior-based control systems—largely lacking specialized selection mechanisms; the emergence of bilaterians may have forced the evolution of a central ganglion, or 'archaic brain', whose main function is to resolve conflicts between peripheral systems. Whilst vertebrates have many interesting selection substrates it is likely that here too, the evolution of centralized structures such as the *medial reticular formation* and the *basal ganglia* may have been a forced move due to the need to limit connection costs as brains increased in size.

Keywords: action selection, nervous system evolution, design space, computational neuroscience, behavior-based robots, Precambrian trace fossils.

---

[*] To appear in the journal *Adaptive Behavior*.

1 Introduction

Action selection is the task of resolving conflicts between competing behavioral alternatives. This problem has received considerable attention in the adaptive behavior literature (see Maes, 1995; Prescott, Redgrave, & Gurney, 1999; Prescott, Bryson, & Seth, In Press) building, in part, on earlier research in ethology (e.g. McFarland, 1971, 1989) and neuroethology (e.g. Davis, 1979; Kristan & Shaw, 1997; Kupfermann & Weiss, 2001) where it is also described as the task of 'decision making', 'behavioral choice', or 'motor program selection'. Whichever label is used, it is useful to recognize at the outset that the problem of selecting actions is really part of a wider problem faced by any complete creature, that of behavioral integration—

> "the phenomenon so very characteristic of living organisms, and so very difficult to analyze: the fact that they behave as wholes rather than as the sum of their constituent parts. Their behavior shows integration, […] a process unifying the actions of an organism into patterns that involve the whole individual." (Barrington, 1967, p. 415)

In discussing control systems for mobile robots, Brooks (1994) has emphasized a similar notion of behavioral coherence which he places at the centre of the problem of autonomous agent design. As robots have become more complex, they have naturally gained an increasing variety of actuator sub-systems, many of which can act in parallel. Controlling robots therefore requires the co-ordination, in space and time, of many interacting sub-systems, and the allocation of appropriate resources between them. The problem for control system design is to satisfy these multiple constraints in a manner that maintains the global coherence of the robot's behavior. Given this context, Brooks raised the concern that research directed at the more specific problem of action selection may not lead to automatic progress in the design of systems with behavioral coherence. It may be the case, for instance, that proposed action selection mechanisms will not scale-up to the task of controlling more complex robots; or, that effective action selection will come to be seen as a consequence of maintaining behavioral coherence, rather than as a key element involved in creating it.

What concerns us here, of course, is the question of the decomposition of control, also known as the 'problem of architecture'. Will an effective robot controller have components whose role is recognizably to resolve conflicts between different action sub-systems? Or, is action selection better regarded as an emergent property—the consequence of many and diverse interactions between multiple sub-systems? (and, in this sense, not something to be considered in isolation from other aspects of control). If effective integration is emergent then research on the design of action selection mechanisms *per se* may lead to a dead-end. On the other hand, if action selection or other related aspects of behavioral integration, can be implemented in specialized system components, then some of the advantages of modularity may accrue to the whole design process. Specifically, it may be possible to add/delete/modify different action sub-systems with less concern for the possibility of adverse, system-wide consequences for the maintenance of behavioral coherence.[1]

How are we to decide answers to these questions? The strategy in this article is to attempt a brief survey of some relevant characteristics in the design of natural control systems for complete creatures—animal nervous systems. The focus will be on those aspects of the functional architecture of nervous systems that seem to play an important role in action

---

[1] A full discussion of the pros and cons of emergent and specialized action selection, particular with respect to the notion of modularity, is given in Prescott et al. (1999).

selection, or, more broadly, in behavioral integration. In particular, I will look for evidence of structures that are specialized to resolve conflicts and that seem to have this as their primary function. The absence of such structures would favor the view that action selection is most often the emergent consequence of the interaction of sub-system elements concerned with wider or different aspects of control. Such findings might encourage the pursuit of similar, distributed solutions to the coordination of complex robot control systems. The presence of candidate structures, on the other hand, would favor the view that complex control architectures can have a natural decomposition into components concerned with the sensorimotor control of action, and those concerned with the selection of action. Such findings would suggest a similar strategy for the decomposition of robot control. To anticipate the argument somewhat, I will be making the case that nervous system evolution does show evidence of specialized action selection mechanisms in some complex natural control systems.

The approach taken here is also an evolutionary one in that I will specifically consider animal nervous systems at three different and important grades in the evolution of complex metazoans (multicellular animals). To place what follows in this evolutionary context, figure 1 shows a phylogeny of the major metazoan phyla illustrating some of the principle early events in the evolution of animal body plans and nervous systems.

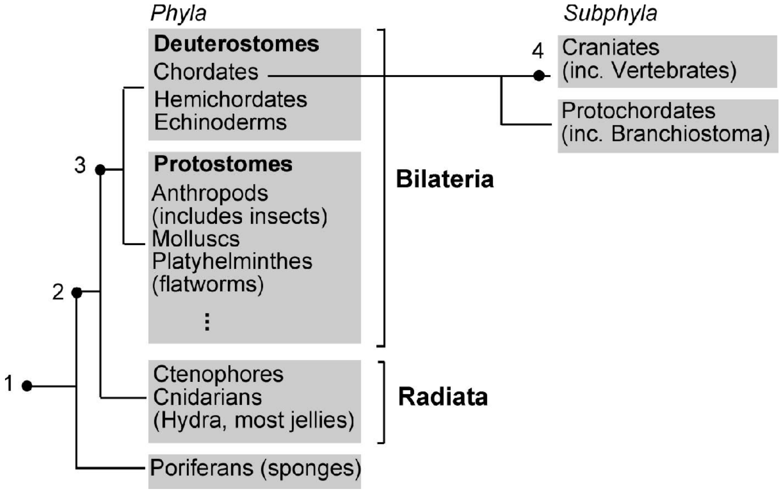

Figure 1. Phylogeny of early metazoans (based on Adoutte et al., 2000; Erwin & Davidson, 2002). Node 1 represents the emergence of multicellularity in aneural, 'colonial' creatures similar to modern day sponges (poriferans). Node 2 marks the appearance of animals with radial symmetry, differentiated cell types, and nerve nets, as exemplified by living cnidarians. Node 3 indicates the emergence of bilaterality along with a more centralized nervous system. Finally, node 4 marks the appearance, within the chordate phylum, of the first *craniate* ancestors of modern vertebrates.

From the perspective of this article, the first event of particular note is the evolution (node 2 in the figure) of neurons and nerve nets in animals similar to those of the extant phylum Cnidaria. This phylum includes a host of mostly simple, but also very intriguing animals such as jellyfish, sea anemones, corals, and hydrozoans (e.g. Hydra). These differ from the most primitive metazoans (Porifera–sponges), in that they possess a variety of different tissue types; generally possess a radial symmetry; may have simple sensory organs; and have nervous systems composed of networks of nerve cells. Fossil evidence suggests that cnidarians were present during the Ediacaran period (635 to 542 mya)[2] at the end of Neoproterozoic era, and are likely to have been the first animals to evolve nervous systems of any kind. There is still a great deal to be learned about the functional architecture of cnidarian nervous systems, however, existing research does provide a number of very interesting pointers. Some of this evidence is reviewed in section 2 below.

The next event, node 3, separates the bilateral animals from the other metazoan phyla. All modern bilaterians possess internal organs, a central nervous system, and a 'brain' formed by an aggregation of neurons towards the anterior end of the animal. On the basis of recent molecular sequencing analyses (see, e.g. Adoutte et al., 2000) it is now thought that the bilaterians divided, at an early stage, into two groups or 'superphyla'—the *protostomes* and the *deuterostomes*. Interestingly, this evolutionary split separates the vertebrates (who belong to the deuterostome chordates) from the protostome invertebrate phyla with more complex nervous systems—arthropods (which includes insects) and mollusks (which includes cephalopods such as the octopi). Of the deuterostomes, in fact, vertebrates are the only animals with highly-developed brains, although the *echinoderms*—such as sea urchins, and starfish—with their pentameral (five-sided) symmetry present some interesting problems (and solutions) in control system design!

Fossil evidence shows a remarkable explosion of animal forms during the Cambrian period (544–488 mya) in which all of the major bilaterian phyla were represented, despite being absent, for the most part, from the fossil record at the end of the Ediacaran. This evidence implies a rapid evolution of complex nervous systems, as part of the general evolution of new body plans (Gabor Miklos, Campbell, & Kankel, 1994); it also indicates that the deuterostome-protostome split predates the Cambrian boundary by some margin. Current hypotheses concerning the last common ancestor of all extant bilaterian groups—the Urbilateria—suggest it was a creature with an anterior-posterior axis, two-ended gut, internal organs, and simple nervous and sensory systems (Baguna et al., 2001; Erwin & Davidson, 2002). More controversially this creature may have had an internal body cavity (coelum), and possibly some simple tentacle-like appendages (Knoll & Carroll, 1999). Genetically, the Urbilateria is thought to have possessed the "essential bilaterian toolbox" (Erin and Davidson, 2002) of regulatory genes, such as the Hox gene cluster, that underlie cell differentiation and body patterning in modern bilaterians. Animals that might fit this description are known to have been dwelling on the sea floor towards the end of the Ediacaran as demonstrated by the large number of trace fossils that have preserved their behavior (e.g. foraging trails) though not their body forms (Crimes & Anderson, 1985; Crimes, 1992; Valentine, 1994). Simulation of these trace fossil patterns indicates a capacity for coordinated behavior not unlike that demonstrated in some simple behavior-based robots (Prescott & Ibbotson, 1997). Section 3 considers some insights into the functional architecture of Ediacaran trace-makers that have been developed through computational modeling. While section 4 reviews neurobiological research on some of the simpler living protostomes (free-living flatworms) whose morphology and nervous system may provide insight into those of the early bilaterians and into the evolutionary origins of the first brains.

Node 4 in figure 1 marks the beginning of a further momentous phase—the evolution within the chordates of the first *craniates*—creatures with a well-developed head and skull, ancestral to all extant vertebrates. Until relatively recently there were no uncontroversial craniate fossils of earlier origin than the Ordovician period (488–444 mya), implying that

---

[2] Dating is from the International Commission on Stratigraphy (http://www.stratigraphy.org/), mya= million years ago. Note that the Ediacaran is also sometimes referred to as the Vendian period.

vertebrates appeared somewhat later than the general explosion of bilaterians. However, finds from Chengjiang in China (the Chinese ‘Burgess shale’) show the presence of fish-like creatures in the early Cambrian (Shu, Luo, & Conway Morris, 1999; Mallatt & Chen, 2003)—between twenty and fifty million years earlier than was previously thought. Evidence from comparative neurobiology (see Prescott et al., 1999 for review) suggests the conservation, through evolution, of a basic vertebrate brain plan that may have been present in early jawless fish (see also Gabor Miklos, 1994; Northcutt, 2002). Taken together, this suggests that the first vertebrate nervous systems may be as ancient as many of those of the protostome bilaterian phyla. Section 5 considers a number of aspects of the functional architecture of vertebrate brains relevant to the problem action selection. This section also briefly outlines some recent efforts to develop computational and robotic models of centralized vertebrate brain structures that play a critical role in action selection and behavioral integration.

Finally, section 6 summarizes this review of the evolution of action selection mechanisms in animal nervous systems and looks for implications that could inspire the design of control architectures for autonomous robots. What exactly do we expect to find? The hope is that the study of comparative neurobiology will uncover evidence of what Dennett (1995) calls ‘forced moves’ in evolutionary design space, that is, outcomes imposed by strong task constraints; or ‘good tricks’—robust and relatively general solutions to common problems, either of which could be usefully transferred into the design space for autonomous mobile beings.

2 Cnidarian nervous systems

Whilst the most primitive metazoans, the sponges, lack neurons and respond only to direct stimulation (usually with a very slow, spreading contraction), cnidarians have quite complex nervous systems, composed, for the most part, of distributed nerve nets, and show both internally generated rhythmic behavior, and coordinated patterns of motor response to complex sensory stimuli.

The basic cnidarian nerve net is a two-dimensional network of neurons that has both a sensory and a motor capacity, and in which there is no distinction between axons and dendrites—nervous impulses therefore propagate in both directions between cells (Mackie, 1990). According to Horridge (1968), in the most primitive nerve nets “the spatial pattern is irrelevant, the connectivity pattern has no restrictions. […] any fiber is equivalent to any other in either growth or transmission” (p. 26).

The lack of intermediary forms of nervous system organization between the aneural sponges and the cnidarian nerve net means that the evolutionary origin of nerve nets, and of nervous tissue in general, is shrouded in mystery. It seems likely, however, that neural conduction was preceded by more primitive forms of communication in which signals were propagated directly between neighboring cells (indeed this form of non-neural communication exists alongside neural conduction in some cnidarians—Josephson, 1974; Mackie, 2004b). The evolution of the nerve net can then be understood as facilitating more rapid and more specific communication over longer distances, which would allow both quicker responses and increased functional diversification between different cell groups (Horridge, 1968; Mackie, 1990).[3] Most of the neurophysiological features of more ‘advanced’ metazoan nervous systems are actually present at the cnidarian grade including multifunctional neurons, action potentials, synapses,

---

[3] Some of the likely benefits of neural conduction have been demonstrated in a computational model of cnidarian evolution developed by Albert (1999).

and chemical neurotransmission. For Grimmelikhuijzen and Westfall (1995) the existence of such features shows cnidarians to be “near the main line” of evolution, and suggests that the study of their nervous systems will illuminate some of the properties of nervous systems ancestral to the higher metazoans.

The nervous systems of extant cnidarians are, in fact, more sophisticated than the above characterization of simple nerve nets indicates. For instance, *Hydra*, one of the simpler living cnidarians, has a variety of different neuronal cell-types, and while most belong to diffuse networks, some are found in localized, well-defined bundles that may have specific functional roles (Josephson & Mackie, 1965; Mackie, 1990). In other cnidarians, such as the hydrozoan jellyfish, parts of the nerve net are fused to form longitudinal or circular tracts that allow very fast signal conduction and can support fast attack or escape reactions. Many of the free-living cnidarians also possess light-sensitive and gravity-sensitive organs that allow behaviors such as orientation, sun compass navigation, and daily migration (see, e.g. Hamner, 1995); unfortunately, for most animals, the neural substrate that supports such behaviors remains poorly understood.

What is known about the functional architecture of cnidarian nervous systems? Pioneering research by Romanes (1885), extended by Horridge (1956; 1968), described the decomposition of the nervous system of the scyphozoan jellyfish *Aurelia aurita* into two distinct components: a network of bipolar neurons that controls the symmetrical, pulsed contraction of the bell and enables the animal to swim; and a second, more diffuse network, consisting largely of small multipolar neurons, that is spread across the body, tentacles, and margins of the animal, and coordinates localized feeding movements. These two systems, which are illustrated in figure 2 for the larva of *Aurelia aurita*, have relatively few interconnections and show clear evidence of independent operation. A similar functional subdivision of the nerve net into two or more parts has also been noted in a variety of other cnidarians such as sea anemones. This behavioral decomposition of control, with physically distinct circuits for feeding and movement, clearly shows an interesting similarity to that proposed for behavior-based robots (see, e.g. (Brooks, 1991; Mataric, 1997).

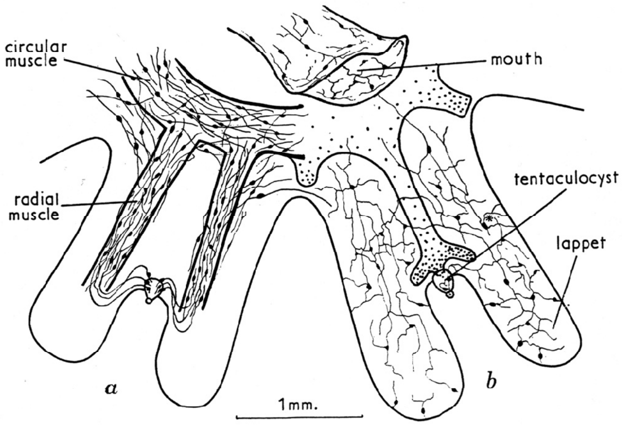

Figure 2. Nervous system of the ephyra larva of *Aurelia aurita*, showing, in two arms of the bell, a) the swimming network controlling the circular, and radial muscles; b) the diffuse nerve-net underlying feeding behavior. A rhopalium (or marginal ganglion) is located at the base of each tentaculocyst. From Horridge (1956). (Reprinted with permission from the Company of Biologists Ltd.)

The question arises, however, are alternative decompositions of the nervous system possible? Meech (1989) describes a hydrozoan jellyfish, *Aglantha digitale*, in which the giant motor axons innervating its swimming muscles can carry two different types of action potentials enabling either rapid escape swimming, or, slow rhythmic swimming for feeding. Similarly, the sea anemone *Actinia*, uses impulse patterns of different frequency to obtain distinct feeding and escape behaviors from a single nerve net (Mackie, 1990). Thus, there seems to be no strong requirement for distinct neural substrates for different classes of behavior in these animals.

The radial shape and relative lack of centralized nervous system components in cnidarians also leads to some interesting and elegant solutions to the problem of generating an integrated global response. For instance, consider the fast escape behavior that can be triggered in some hydromedusan jellyfish by contact at any point on the periphery of the animal. Since jellyfish swim by the synchronous, simultaneous contraction of the entire perimeter of the bell, the lack of centralized signaling presents an interesting control problem for which Mackie (1990) describes two contrasting solutions. One solution, seen in *Aglantha*, uses giant axons with very fast conductance so that a single spike can circumnavigate the periphery in just a few milliseconds. An alternative and perhaps more remarkable solution, seen in the much larger species *Polyorchis*, involves a network of neurons (the Swimming Motor Neurons) that carries action potentials that change shape as they circle the bell. Successive muscles groups respond to these changing shapes by contracting at shorter and shorter latencies, thus ensuring a uniform and synchronized contraction of the whole perimeter. This elegant solution appears to depend solely on membrane-level properties of the neurons involved (Spencer, Przysiezniak, & Acosta-Urquidi, 1989).

According to Horridge (1956) (see also Satterlie, 2002) the two functionally distinct nerve nets of *Aurelia aurita* make contact with one another in eight neuron clusters termed the marginal ganglia or *rhopalia*. Each rhopalium is part of the swimming network and is involved in the regular beat of the swimming contraction; it can also generate its own regular pulse if isolated from other parts of the network (thus showing an intrinsic rhythm generating capacity). Each rhopalium is also in contact with the diffuse network that underlies the feeding response. Excitation in the diffuse network can inhibit the swimming rhythm or, in some cases, accelerate the rhythm. This evidence suggests a hierarchical arrangement: pattern formation (the swimming beat) seems to be under the distributed control of multiple pacemaker systems (see Satterlie, 2002, for a discussion of how they interact), whilst the behavior of this swimming network is under the modulatory control of the diffuse feeding network. If this is the case, then this jellyfish nervous system could be viewed as providing a natural example of a *subsumption architecture*[4] (Brooks, 1986) composed of two distributed layers of control.

In *Aglantha digitale*, which is thought to have the most complex neural circuitry of known Cnidaria, twelve distinct neuronal circuits and two epithelial (cell-to-cell) conduction systems have been identified (Mackie, 2004a). Interestingly, as this animal (and other hydromedusan jellies) evolved from a creature with a more distributed wiring plan, a form of centralization has occurred with much of the neural circuitry becoming compressed into two marginal, nerve rings that have thus taken on some of the characteristics of a central nervous

---

[4] A subsumption architecture is one in which control is decomposed into distinct layers where higher layers are able to modulate the outputs of lower ones (e.g. by adjusting gain), or replace the outputs of lower layers with their own signals. When a higher layer of control is removed of damaged the lower layers are still able to function, however, the reverse is not true; competencies implemented by higher layers rely on the integrity of lower ones in order to function (see Brooks, 1986; Prescott et al., 1999 for further explanation).

system (Satterlie, 2002; Mackie, 2004a). Much is now known about the functional roles of each of the control sub-systems and their interactions (Mackie & Meech, 2000; Meech & Mackie, 2001), making this animal an enticing prospect for future computational modeling. From the perspective of this review the following features are of particular note. First, the circuitry underlying slow swimming and fast escape share some common neural substrates (e.g. the giant motor axons noted above), but also have some distinct elements. For instance, slow swimming involves a network of "pacemaker" neurons in the inner ring cord that, in addition to generating the swimming rhythm, help to induce slow regular contractions in the tentacles via a circuit known as the "relay system". Escape, on the other hand, involves a network of "ring giant" neurons in the outer nerve ring in which activation can be triggered by deflection of sensitive hair cells. This system can initiate rapid contraction of the tentacles to accompany the fast swimming response. However, these two circuits also interact, such that, for instance, activity in the pacemaker and relay systems can initiate spiking in the ring giant that will cause escape-like, rapid tentacle contraction during slow swimming. The uniformity of the ring nerve system as it circumnavigates the bell, and the existence of many substrates that allow interactions between the underlying circuits, indicate that there is no specialized substrate for action selection in this animal. The fast escape circuit clearly has the ability to override regular swimming, however, the capacity of the latter to co-opt escape circuitry for its own uses means there is a comparatively complex mapping from the functional architecture of this animal to the underlying neural substrate.

Aurelia and *Aglantha* provide contrasting examples of jellyfish control systems that to some extent typify the scyphomedusan and hydromedusan groups to which they belong (Satterlie, 2002). A third group, the cubomedusans (or box jellyfish*)*, are also worth noting. Like the scyphomedusans these animals have distinct ganglia (rhopalia) that generate the swimming pattern, though the number of these structures is reduced to just four; however, like the hydromedusans the box jellies also have a condensed nerve ring that directly connect the rhopalia together—presumably allowing for faster, targeted transmission (Satterlie, 2002). The rhopalia themselves are also comparatively complex in that each carries four 'eyes', two of which include both a lens and a retina and that are probably capable of some form of spatial vision (Nilsson, Gislen, Coates, Skogh, & Garm, 2005). The cubomedusae are known to be agile swimmers, that may actively pursue prey, and the rhopalia, as pacemakers, appear to interact in a more complex and semi-independent manner than in other jellyfish allowing asymmetrical contractions that provide increased maneuverability (Satterlie & Nolen, 2001).

In sum, cnidarian nervous systems demonstrate the ability of relatively simple nerve networks to support multiple behavioral modes, in some cases, using the same neural structures to generate two quite different patterns of activity. Behavioral decomposition of function seems to be significant trait in simpler animals, and the distributed nature of many cnidarian nervous systems would seem to make them a good preparation in which to study behavioral integration as a more global property of the control system architecture. At the same time, however, the condensation of nerve nets into nerve rings in both hydro- and cubo- medusae, and the reduction of the number of rhopalia in the latter[5], would suggest that even in radially symmetric creatures, enhanced behavioral complexity requires a degree of centralization of control. This trend would appear, then, to have the characteristics of one of Dennett's "forced moves". Indeed, Satterlie, referring to the shared characteristics of hydrozoan and cubozoan swim systems, expresses a similar thought—"hydrozoan-like specializations [including the presence

---

[5] Satterlie (2002) discusses comparative data suggesting that both nerve rings and the reduced number of rhopalia in cubomedusans are derived features rather than primitive cnidarian traits.

of the ring nerve] may well be examples of convergence of traits that are essential to highly efficient, directed locomotion” (Satterlie, 2002, p. 1666).

3 Robot modeling of the behavior of early bilaterians

As noted above, the common ancestor of all modern, bilaterally symmetric animals, was probably a bottom-dwelling creature, living in a shallow marine environment during the mid- to late- Ediacaran period. Such animals, along with many of the early bilaterians (worms, mollusks, and arthropods) they gave rise to, will have left no or few actual fossils as they had virtually no hard body-parts. Fortunately, however, they did leave a fossil record of sorts—the tracks, trails, and burrows of many early invertebrates have been preserved forming what are now called trace fossils. The earliest foraging trails, which are sometimes called ‘scribbles’, show tracks that often cross themselves, and indicate relatively crude foraging strategies. By the end of the Ediacaran, however, more regular foraging patterns were appearing that formed spiral fossils or ‘meandering’ trails that loop back on themselves without crossing (Crimes & Anderson, 1985; Crimes, 1992). One such fossilized meander is shown in figure 3.

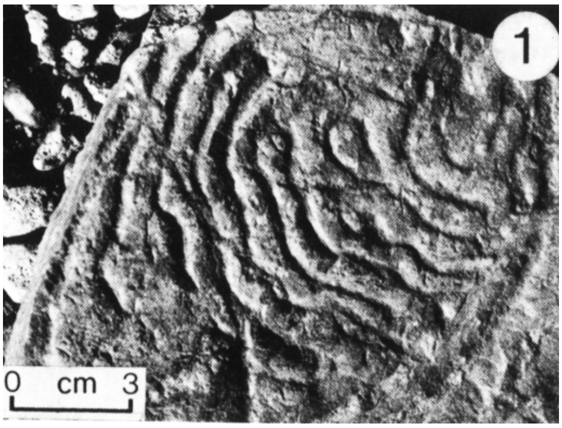

Figure 3. An Ediacaran meandering trace fossil (Crimes & Anderson, 1985). Reprinted with permission from SEPM (The Society for Sedimentary Geology).

In attempting to infer the behavioral capabilities of the ancient animals that left these fossil traces, it seems reasonable to seek the simplest mechanisms that will reproduce the observed patterns. In 1969, the geologists Raup and Seilacher published an article demonstrating that computer simulations of meandering trace fossil patterns could be created by combining a number of simple reactive behaviors: *thigmotaxis*, stay close to previously formed tracks; *phobotaxis*, avoid crossing existing tracks; *strophotaxis* make 180° turns at various intervals; and move forward (*advance)* when the conditions of the other behaviors are not met. The principle of a complex behavior pattern emerging from the interaction of a number of simple reactions is a characteristic that this early work in computer modeling clearly shares with the 'behavior-based' approach in robotics. Indeed, Raup and Seilacher’s meander generator bears striking similarities to many of the 'wall-following' mechanisms that have been used in the control of behavior-based robots. For instance, Mataric (1990) describes a robust wall-following behavior that emerges from the interaction of three modules. The first, similar to thigmotaxis, causes the robot to steer inwards (toward the wall) when sensors indicate that the distance to the wall is above some threshold; the second, similar to phobotaxis, causes the robot to steer outwards when the sensed distance is below a threshold; while, the third, causes the robot to move forward whenever the conditions of the other two behaviors are not met.

This fascinating intersection between evolutionary biology and robotics inspired Carl Ibbotson and I to make our own investigations into robot trace-making behavior using a custom-built robot that could generate and follow trails across the laboratory floor (Prescott and Ibbotson, 1997). The sediment feeders of the Precambrian probably used chemical and mechanical sensory systems to detect and follow their tracks and burrows, however, as a (very) loose approximation to these mechanisms our robot used light sensors to detect a trail of paper which was dispensed by the robot as it moved across the laboratory floor. Figure 4 shows how the different component reactions required for (paper) trail-making can be easily implemented by a robot.

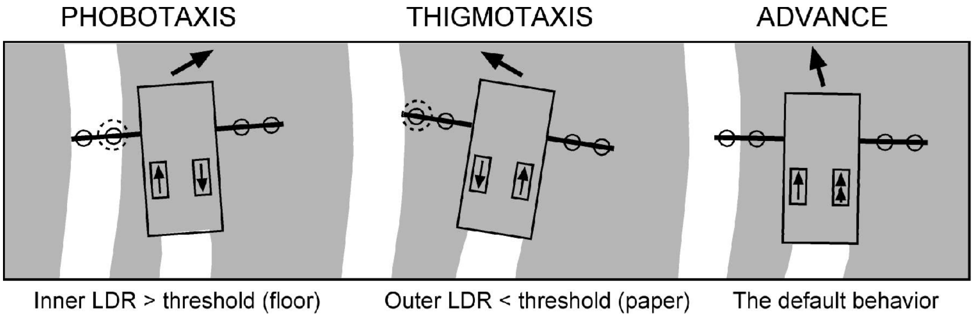

Figure 4. Implementing trail-making behavior in a robot. The robot has two arms (right and left) each carrying two light sensors (LDRs) and two motors (right and left). *Phobotaxis* (left), a turn away from the sensor arm, is triggered when the value of the inner LDR sensor is greater than a threshold set slightly above the reflectance of the dark floor surface. *Thigmotaxis* (center), a turn towards the sensor arm, is triggered when the value of the outer LDR sensor is less than a threshold set slightly below the reflectance of the light-colored paper dispensed by the robot. In both cases the required turn is achieved by rotating the drive wheel on the outside of the turn forwards, and that on the inside of the turn in reverse. For the *advance* behavior (right) the robot moves forward on a trajectory that drifts inwards towards the sensor arm. (From Prescott & Ibbotson, 1997).

The three behaviors illustrated in figure 4—phobotaxis, thigmotaxis, and advance—are sufficient to generate a *spiraling* trail provided two action selection issues are addressed.

First, the phobotaxis behavior should take priority over thigmotaxis when the sensory pre-conditions for both behaviors are met as this will prevent the robot from re-crossing a narrow section of its early path. Indeed, based on their study of different forms of trace fossil meander, Raup and Seilacher argued that thigmotaxis and phobotaxis were "genetically distinct behavioral reactions". Following this precedent, the elements of the robot control system were conceived of as distinct competencies, arranged in a subsumption-like hierarchy, with phobotaxis able to suppress thigmotaxis which, in turn, suppresses advance (see Figure 6 below).

Second, the robot should be controlled by just one of its two sensor arms—the robot will then spiral in the direction of that arm; otherwise, with both arms active, the two sides would send conflicting signals to the motors causing the robot to move off-course. The control architecture must therefore select a dominant side and suppress motor control signals arising from the opposite side.

In order to generate a *meandering* trail, that is one containing U-turns, an additional *strophotaxis* mechanism is needed that will swap control of the robot from one sensor arm to the other at appropriate moments. Figure 5 shows the meandering trail generated by a robot that uses ‘time outs’ to control strophotaxis, in other words, control is swapped between the two sides of the robot at fixed time intervals[6]. Figure 6 illustrates the functional architecture, just described, for the embedded controller. A behavioral hierarchy is implemented on each side of the robot to control responses to local sensory signals, while strophotaxis sub-systems bridge the robot ‘midline’ in order to regulate which side has control of the motors at any given time.

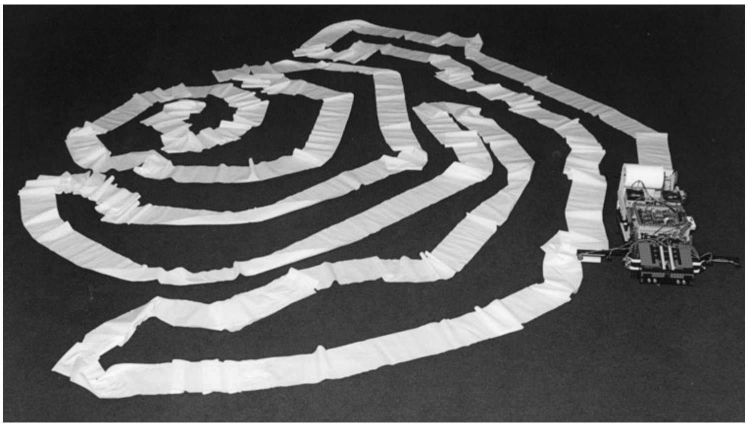

Figure 5. A robot meander. Control is passed from one side of the robot to the other every thirty seconds. As soon as control is swapped from one side to the other, the self-correcting nature of the thigmotaxis/phobotaxis reactions causes the robot to turn until contact is regained with the trail on the opposite side. Hence, the U-turn itself is not explicitly programmed. Note also the ‘starter spiral’ which is the result of ‘trail following’ where there is no initial trail to follow. Similar starter spirals are seen in many meandering trace fossils. (Photograph from Prescott & Ibbotson, 1997).

The functional architecture just described for the robot meander, suggests that sensorimotor control in early bilaterians may have also combined reactive systems capable of responding to local (unilateral) stimuli, with control elements that act more globally in determining the behavioral strategy of the whole organism. I will return to the question of what this might imply about the substrate for behavioral integration in these animals after considering some potentially relevant clues from invertebrate neurobiology.

---

[6] See Prescott and Ibbotson (1997) for a discussion of the likely triggers for strophotaxis events in trace fossil meanders.

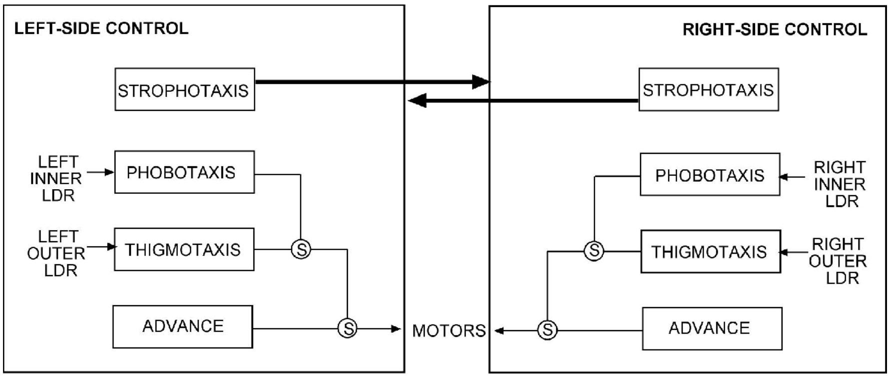

Figure 6: An architecture for generating meandering trails. The functional sub-systems for trail-making are arranged in two unilateral hierarchies that generate motor signals targeting a shared set of motors. The strophotaxis sub-systems provide communication and arbitration between the two sides of the robot, switching control of the motors from one side to the other at regular time intervals, and preventing the outputs of the non-active side from reaching the motor resource. (From Prescott and Ibbotson, 1997).

4 Flatworm nervous systems

In the evolution of bilateral animals a critical development was the appearance of a central nervous system organized around a massed concentration of nerve cells called the *cephalic ganglion*, or ‘archaic brain’. In flatworms—animals of the phylum *platyhelminthes*—we find the simplest living animals that possess this form of nervous system architecture (Reuter, 1989; Reuter & Gustafsson, 1995).

Traditional phylogenies placed platyhelminthes as the start of the bilateral radiation as a stem phylum from which both the protostome and deuterostome groups later evolved. Recent molecular analyses have, however, generated a rather more complex picture. Specifically, it is now thought that the majority of flatworm classes belong within the protostome group and therefore have no special claim to be representative of the first bilaterians (Adoutte et al., 2000). On the other hand, there is also evidence to suggest that a sub-group of platyhelminthes—the acoel flatworms (Acoela)—are sufficiently distinct from other protostomes as to be a possible ‘sister group’ to the bilaterians and therefore an important source of insights into the likely characteristics of a common ancestor (Ruiz-Trillo, Riutort, Littlewood, Herniou, & Baguna, 1999; Baguna & Riutort, 2004; Ruiz-Trillo, Riutort, Fourcade, Baguna, & Boore, 2004). Indeed, the acoels, may be somewhat simpler than the Urbilateria, based on estimates of the morphology of that creature, reflecting the fact that bilaterality, as a trait, will likely have appeared some time earlier than the protostome-deuterostome divergence (Knoll & Carroll, 1999). Whilst the debate about the status of the Acoela has yet to be fully resolved[7] it remains the case that flatworms are, morphologically, among the simplest bilaterian

---

[7] Adoutte and colleagues (Adoutte et al., 2000; Balavoine, de Rosa, & Adoutte, 2002) have proposed a contrary view that includes the acoels within the protostome group, rather than as a sister group to the bilaterians.

animals and that therefore an investigation of their neurobiology could provide useful insights into the early evolution of bilateral nervous systems. Unfortunately, although the acoels may be the most primitive of the flatworms, the literature on their neurobiology is limited and mostly confined to anatomical studies. One significant conclusion that has been drawn from the available data is that the cephalic ganglia of acoels are surprisingly varied: a finding that suggests that primitive brains may have evolved from undifferentiated nerve nets on a number of separate occasions (Raikova et al., 2004). Given the lack of functional studies in the acoel flatworms, I will look here at findings from another group of free-living flatworms—the polyclad turbellarians—in order to gain some insights into the relationship between brain and behavior in animals of flatworm grade. Although probably belonging to different phyla, it has been noted that acoels and turbellarians share similarities in the ways their nervous systems have evolved (Raikova et al., 2004). Such convergences imply that similar constraints may be at work, leading to the possibility of uncovering a further "forced move".

Turbellarian flatworms range in size from a few millimeters to tens of centimeters. They are found in aquatic environments or moist terrestrial environments where most pursue a predatory or scavenging life-style requiring a repertoire of reasonably complex behaviors. Like other bilaterians, these animals have distinct anterior and posterior ends, and dorsal (upper) and ventral (lower) surfaces. Sensory systems are distributed symmetrically between the left and right sides of the body, but together with the nervous system often show a concentration, termed *cephalization*, towards the anterior end of the body. Turbellarian nervous systems (like the acoels) appear in a bewildering variety of different configurations, none of which can necessarily be considered primitive (Reuter, 1989). Typically, there are three to five pairs of major nerve cords connecting with the cephalic ganglion (see, e.g. figure 7). These cords are interlinked by circular commissures (bands of nerve fibers), which themselves make connections with networks (plexuses) of nerves underlying muscular and/or epithelial tissue. The cell bodies of sensory neurons are found near the periphery while those of motor neurons and interneurons are distributed throughout the nerve cords and the brain. The concentration of nerve cells into cords, fibers, and ganglia distinguishes this type of central nervous system from the nerve nets of the simpler cnidarians. The following discussion of the functional architecture of the flatworm nervous system follows the research of Gruber and Ewer (1962) and of Koopowitz and co-workers (Koopowitz, 1970; Koopowitz, Silver, & Rose, 1975; Koopowitz, Silver, & Rose, 1976; Koopowitz & Keenan, 1982; Koopowitz, 1986, 1989) that has focused on the role of the brain in marine polyclad turbellarians.

Gruber and Ewer studied the effect of brain removal on the behavior of the polyclad *Planocera gilchristi*, whose nervous system is pictured in figure 7. This animal usually moves by swimming or crawling along the substrate. Swimming involves the generation of a transverse wave that moves backwards along the length of the body, while crawling involves a regular alternating extension of the two sides of the body. Following brain removal, Gruber and Ewer reported that components of both normal swimming and normal crawling were present in decerebrate worms but that these were never integrated into the normal sequences—the overall movement of the animal was irregular and uncoordinated. Similarly, decerebrates lacked a normal rapid righting response when placed in an inverted position, although they could eventually right themselves by making writhing and twisting movements. These animals also failed to display the normal retraction response to mechanical stimulation, again responding with an uncoordinated writhing.

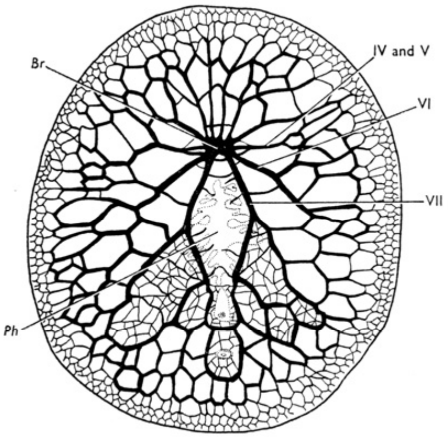

Figure 7. Nervous system of the turbellarian *Planocera gilchristi*, viewed from above, showing the brain (Br), pharynx (Ph), and major nerve cords (1V-VII). The anterior of the animal is towards the top of the picture. The finest granularity of nerve fibers is only shown in the central areas around the pharynx. From Gruber and Ewer (1962). (Reprinted with permission from the Company of Biologists Ltd.)

Gruber and Ewer also describe the effects of decerebration on the feeding behavior of *Planocera*. This behavior was the subject of further detailed investigation by Koopowitz (1970) who went on to examine decerebrate feeding in another marine polyclad—*Notoplana aticola* (Koopowitz et al. 1975, 1976). The behavior of *Notoplana* will be described as it is typical of the general pattern of results obtained with these animals.

In the intact polyclad worm presentation of a food item near to its posterior margin will cause it to extend a nearby portion of that margin and use this to take hold of the food. The animal will then rotate the anterior part of its body on that side, until the anterior margin comes into contact with the food. The posterior margin subsequently loosens its grip allowing the anterior edge to manipulate the food into the mouth. This sequence of behavior is shown in figure 8a. When fed with large food items (dead shrimps) the animal becomes satiated after a few food presentations and the feeding response ceases.

In the decerebrate animal, in contrast, the body turn to bring the anterior margin into contact with the food is never observed. Instead, the animal performs a ‘local feeding response’ in which it gradually moves the food directly to its mouth via the underside of its body (figure 8b). In addition to the lack of a coordinated ‘whole body’ feeding response the decerebrate animals show no satiety and will continue passing food items towards the mouth even once the gut is completely full. Control experiments in which the brain remains intact but the main posterior nerves on one side of the body are severed, show feeding behavior characteristic of the normal animal on the intact side, and that characteristic of the decerebrate on the cut side.

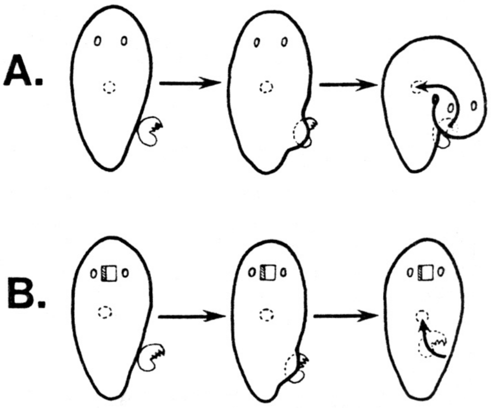

Figure 8. Feeding behavior of the polyclad *Notoplana*. A. In the intact animal contact with an item food at the posterior margin causes a whole body response in which the animal turns and grabs the food with its anterior edge before passing it to the central, ventrally located mouth. B. In the decerebrate animal, a 'local feeding response' causes food to be passed directly to the mouth. From Koopowitz and Keenan (1982). (Reprinted with permission from Elsevier Science.)

Overall, these experiments on decerebrate polyclad behavior demonstrate the role of the brain in regulating local reflexive actions whose neural substrate is located in the periphery of the animal. In the case of crawling and swimming, the brain orders the temporal sequence of local activity in different marginal areas of body. In the case of feeding, the brain holds the 'local feeding response' under inhibitory control whilst enabling actions involved in the 'whole body' feeding response.

This centralized coordination of behavior seen in the polyclad stands in interesting contrast to the more distributed nature of control noted in cnidarians. What evolutionary pressures may have brought about such a change in the functional organization of nervous systems? Koopowitz and Keenan (1982) contrast two possible explanations for the evolution of the first brains. The first possibility is that the brain is one of several consequences of the process of cephalization—the aggregation of sensory systems in the anterior portion of the animal. According to this explanation, the co-ordination of peripheral mechanisms becomes focused in the brain in order to place it closer to the principle sources of afferent stimulation. This view also makes the primary role of the primitive brain one of response initiation. The alternative view, favored by Koopowitz and Keenan, is based on the observation that although all polyclads have brains, not all show significant cephalization. Instead, the origin of the brain could be attributable to a more fundamental change in the body plan of the organism—the evolution of bilateral symmetry itself:

> "We consider that the development of bilateral symmetry, rather than cephalization, was the prime feature that necessitated the evolution of the brain. Bilateral symmetry required that the right-hand side know what was happening on the left, and vice versa. In effect, with the advent of bilateral symmetry, the evolution of the brain was necessary for the coordination of disparate peripherally-based reflexes. This was of prime importance in preventing the two sides from engaging in contradictory activities." (Koopowitz and Keenan, 1982, p. 78)

From the perspective of this paper, this interesting proposal might be paraphrased as the hypothesis that the brain first evolved as a centralized substrate for action selection. While in the more 'advanced' Cnidaria there is evidence of the condensation of nerve nets into specialized neural control structures (such as the nerve rings); in flatworms the evolution of dedicated conduction pathways (such as nerve cords) combines with an opportunity, denied to the bag-like jellies, of placing a coordinating center at a strategic position along the midline and towards the anterior end of the animal.

In anatomical studies of the polyclad brain, Koopowitz and colleagues (see Koopowitz, 1986) were able to identify, by dye-staining, many *decussating* neurons—cells whose soma and dendritic trees were found in one half of the brain while their axons projected across the midline to peripheral targets on the other side of the body. A subset of these neurons were also found to be electrotonically coupled with symmetrical cells on the opposite side of the midline (meaning that cell pairs will work in unison). Decussating neurons could provide a key element of the substrate for maintaining behavioral coherence between the two halves of the body: non-coupled neurons acting, where required, to suppress or facilitate responses in the opposite body-half; coupled neurons operating when there is a need to ensure synchrony between the two sides.

Koopowitz and co-workers (1970, 1982, 1989) also describe further experiments in which half of the polyclad brain is excised, and the severed cephalic nerve cords allowed to regrow, re-establishing appropriate functional connections with the remaining half-brain. In other experiments the brain of one animal is transferred in its entirety into another's body and once again re-exerts many of its original behavioral controls over the periphery. Finally, brain-control returns even if the brain is re-inserted upside-down or rotated 180° (try doing this with a robot's CPU!). This robustness of function is particularly remarkable given that the brain is clearly much more than a relay station between the two halves the animal, but instead plays an integrative role in selecting appropriate patterns of peripheral motor acts.

4.1 Precambrian trace-makers revisited

We are now in a position to reconsider the 'meander' control system of the model Precambrian trace-makers in the light of this evidence concerning the evolution and function of the 'archaic brain'. Recall that the core components of the meander generator, the thigmotaxis and phobotaxis reactions, are reflexive mechanisms associated with peripheral sensors. However, a further crucial part of the control system is the component that determines which side of the body is actively controlling the motor system, or that switches control from one set of peripheral mechanisms to another (strophotaxis). As noted above, for Koopowitz and Keenan, the flatworm brain, with its networks of decussating neurons, is primarily a mechanism that prevents the two sides of the body "from engaging in contradictory activities". It is possible to speculate, then, that this might also have been true of the nervous systems of the early, meandering fossil makers. In other words, that the appearance of efficient spiraling and meandering foraging trails in the fossil records of the late Ediacaran may mark the point where centralized action selection mechanisms had evolved to take control over peripheral reflexive systems.

5 Vertebrate nervous systems

The origin of the vertebrate nervous system is in some respects an unsolved problem in evolutionary neurobiology (Northcutt, 2005). Vertebrates belong to the phylum Chordata whose members all possess, at some stage in their development, a single, hollow nerve cord, called the neural tube, which runs most of the length of the longitudinal body axis. Unfortunately, all living protochordates (that is, animals of the chordate phylum that are *not* craniates) have relatively simple nervous systems, and only one species, *Branchiostoma* (previously known as *Amphioxus*), has a nervous system that could resemble a transitional stage between ancestral chordate and vertebrate. *Branchiostoma* shows elaborations at the anterior end of the neural tube that may be homologous to some regions of the vertebrate brain (Lacalli, 1996); however the 'brain' of *Branchiostoma* is tiny, its sensory systems primitive, and its behavior very simplified compared with that of living vertebrates. In the modern fauna, the most primitive craniate characteristics are found amongst the jawless fish (Agnatha) (Northcutt, 1996). Examination of these animals has shown the same gross morphological divisions of the nervous system—spinal cord, hindbrain, midbrain, and forebrain—as are present in other vertebrate classes. Indeed, impressions of these structures have also been found in the fossilized endocasts (casts from the inside of fossil skulls) of ancient agnathans (Halstead, 1965). This evidence suggests that a basic 'ground plan' for the nervous system is shared by all living vertebrate classes, and possibly by all ancestral vertebrates (see Prescott et al, 1999; Northcutt, 2002).

The substrate for action selection in a control architecture as complex as the vertebrate nervous system is likely to involve many different mechanisms and structures. The following brief review is by no means exhaustive but considers a few promising candidates.

5.1 Conflict resolution for clean escape

One of the requirements for effective action selection is timely, sometimes very rapid, decision making. Transmission and response times in neural tissue are not negligible so for urgent tasks it is important to ensure that time is not lost resolving conflicts with competing behaviors. Indeed, there is evidence to suggest, that for tasks such as defensive escape, special circuitry may have evolved in the vertebrate nervous system to provide a very fast override of the competition. The giant *Mauthner* cells (M-cells) found in the brain-stem of most fish and some amphibians provide an example of this function (Eaton, Lee, & Foreman, 2001). M-cells are known to be involved in the 'C-start' escape maneuver—the primary behavior used by many species of fish to avoid hazards such as predation. Eaton, Hofve, and Fetcho (1995) have argued that the principle role of the M-cell in the brainstem escape circuit may not be to initiate the C-start as much as to *suppress competing behaviors*. This conclusion is supported by evidence that removal of the M-cells does not disable the C-start and has only a mild effect on the strength or latency of the response. Instead, the fast conduction of the Mauthner giant axon (one of the largest in the vertebrates) may be crucial in ensuring that contradictory signals, that could otherwise result in fatal errors, do not influence motor output mechanisms. Conservation of brain-stem organization across the vertebrate classes suggests that homologous mechanisms may play a similar role in the escape behaviors of other vertebrates (Lingenhohl & Friauf, 1994; Eaton et al., 2001).

5.2 Fixed priority mechanisms

Many studies of the role of the vertebrate brain in behavioral integration suggest that the resolution of conflict problems between the different levels of the neuraxis (spinal cord, hind-brain, mid-brain, etc.) may be determined by fixed-priority, vertical links. For instance, Prescott et al. (1999) have reviewed evidence that the vertebrate defense system can be viewed as a set of dissociable layers in which higher levels can suppress or modulate the outputs of lower levels using mechanisms somewhat similar to the inhibition and suppression operators employed in the subsumption architecture. Fixed-priority mechanisms cannot, however, capture the versatility of behavior switching observed between the different behavior systems (defense, feeding, reproduction, etc.) found in adult vertebrates. Since dominance relationships between behavior systems can fluctuate dramatically with changing circumstances more flexible forms of selection are required than can be determined by hard-wiring.

5.3 Reciprocal inhibition

A specific form of neural connectivity, often associated with action selection, is mutual or reciprocal inhibition (RI). In networks with recurrent reciprocal inhibition two or more sub-systems are connected such that each one has an inhibitory link to every other. Such circuits make effective action selection mechanisms since the most strongly activated sub-system will receive less total inhibition than any of the others; and the recurrent connectivity of the system results in positive feedback that rapidly maximizes the activity of this ‘winner’ relative to all the other ‘losing’ sub-systems. RI connectivity has been identified in many different areas of the vertebrate brain (Windhorst, 1996) and could play a role in conflict resolution at multiple levels of the nervous system (Gallistel, 1980). For instance, RI between the ventrolateral preoptic (VLPO) nucleus of the hypothalamus and a group of monaminergic brainstem nuclei has been found to play a critical role in regulating mammalian sleep-wake behavior (Saper, Scammell, & Lu, 2005). VLPO neurons that are primarily active during sleep have direct, mutual inhibitory connections with cells in these monaminergic nuclei that fire most rapidly during wakefulness; the resulting circuit instantiates a ‘flip-flop switch’ capable of generating rapid transitions between arousal states. A further group of neurons in the lateral hypothalamus modulates the stability of this switch which would otherwise be over-sensitive to small perturbations.

5.4 Centralized selection mechanisms

Snaith and Holland (1990) have contrasted distributed action selection based on RI with a system that employs a specialized, central switching device. They note that to arbitrate between n competitors, an RI system with full connectivity requires $n(n-1)$ connections, while adding a new competitor requires a further $2n$ connections. In contrast, a system using a central switch requires only 2 connections per competitor (to and from the switch) resulting in $2n$ connections in all. Adding a further unit requires only 2 additional connections. On this comparison, a central switching device clearly provides a significant advantage in terms of economy of connections costs. Ringo (1991) has pointed out that geometrical factors place important limits on the degree of network interconnectivity within the brain. In particular, larger brains cannot support the same degree of connectivity as smaller ones—significant increases in brain size (as have been seen in vertebrate evolution) must inevitably be accompanied by decreased connectivity between non-neighboring brain areas. Since, during awake behavior, functional units in different parts of the brain will often be in competition for the same motor resources, the requirement of lower connectivity with increased brain-size would appear to favor selection architectures with lower connectional costs than RI. Below I consider two brain sub-systems—the *basal ganglia* and the *medial reticular formation*—that may have evolved as centralized selection mechanisms to meet this need.

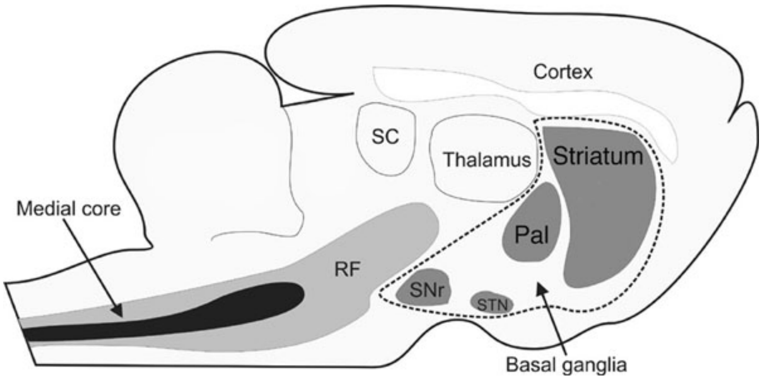

Figure 9. Systems for action selection in the vertebrate brain: A saggital slice through the rat brain illustrating the locations of medial core of the reticular formation (mRF), the basal ganglia (Striatum, Pal—Pallidum, SNr—Substantia Nigra, STN—subthalamic nucleus), and the superior colliculus (SC).

5.4.1 The basal ganglia

The principle components of the basal ganglia include the *striatum* and *pallidum* in the base of the vertebrate forebrain, and the *substantia nigra* in the midbrain. These structures (or homologous nuclei) are found in the nervous systems of all classes of jawed vertebrates and possibly in all vertebrates (Northcutt, 1994; Medina & Reiner, 1995). The striatum, in particular, is a substantial structure in all vertebrate brains and occupies a roughly similar proportion of forebrain volume in all the vertebrate classes (Hodos, 1982; Finlay & Darlington, 1995). The proposal that the basal ganglia are involved in action selection is based on an emerging consensus amongst neuroscientists that a key function of these structures is to enable desired actions and to inhibit undesired, potentially competing, actions (e.g. Chevalier & Deniau, 1990; Mink & Thach, 1993; Groenewegen, Wright, & Beijer, 1996; Redgrave, Prescott, & Gurney, 1999; Grillner, Hellgren, Menard, Saitoh, & Wikstrom, 2005). The following provides a brief summary of the proposed functional architecture, a full account of this view has been provided elsewhere (Prescott et al., 1999; Redgrave et al., 1999).

Neural signals that may represent ‘requests for access’ to the motor system are continuously projected to the striatum, which is the principle basal ganglia input nucleus, from relevant functional sub-systems in both the brainstem and forebrain of the animal. Afferents from a wide range of sensory and motivational systems also arrive at striatal input neurons. This connectivity should allow both extrinsic and intrinsic motivating factors to influencing the strength of rival bids. The level of activity in different populations of striatal neurons (*channels*) may then form a “common currency” in which competing requests for actuating systems can be effectively compared. The main output centers of the basal ganglia (parts of the substantia nigra and pallidum) are tonically active and direct a continuous flow of inhibition at neural centers throughout the brain that either directly or indirectly generate movement. This tonic inhibition appears to place a powerful brake on these movement systems such that the basal ganglia seem to hold a ‘veto’ over all voluntary movement. Intrinsic basal ganglia circuitry, together with feedback loops via the thalamus, appears to be suitably configured to resolve the selection competition between multiple active channels and selectively *disinhibit* winning action sub-systems whilst maintaining or increasing inhibition on competing channels.

A large number of computational models, at different levels of abstraction, have now examined the functional capabilities of basal ganglia circuits from the perspective of action selection (see Prescott, Gurney, & Redgrave, 2002; Gurney, Prescott, Wickens, & Redgrave, 2004 for reviews). One of these models has also been instantiated, and demonstrated to be effective, within the control architecture of a small mobile robot (Montes Gonzalez, Prescott, Gurney, Humphries, & Redgrave, 2000; Prescott, Gonzalez, Humphries, Gurney, & Redgrave, 2006). Collectively, these models lend considerable support to the hypothesis that the basal ganglia are suitably connected and configured to serve as an array of specialized central switching devices that could provide effective conflict resolution with economical interconnectivity.

5.4.2 The medial reticular formation

Studies of infants rats in whom the basal ganglia are not yet developed (see, e.g. Berridge, 1994), and in decerebrate animals in which the forebrain and much of the midbrain have been removed (Woods, 1964; Lovick, 1972; Berntson & Micco, 1976), indicate that, below the basal ganglia, there is a brainstem substrate for selection that can provide some basic behavioral switching while the adult architecture is developing or when it is damaged or incapacitated. A likely locus for this mechanism is in the *medial* core of the brainstem *reticular formation (mRF)* (Scheibel & Scheibel, 1967; Scheibel, 1984; Humphries, Gurney, & Prescott, In Press). The mRF appears to fulfill the connectional requirements of a centralized selection system in that it receives afferent input from all of the body's external and internal sensory systems and projects outputs to the cranial nerves that control movement of the face and to spinal neurons that command limb control and locomotion pattern generation. The intrinsic circuitry of the mRF appears to be configured as a set of clusters, that the Scheibels (1967) analogized with "a stack of poker chips". In each cluster there are two main neural populations: the first consists of large projection neurons, having excitatory outputs, that branch to targets in the spinal cord and midbrain as well as to other cluster within the mRF; the second population consists of inter-neurons that project inhibitory outputs entirely within the same cluster. Humphries, Gurney, & Prescott (2005) have shown that the structure generated by this pattern of intrinsic connectivity is that of a 'small-world' network (Watts & Strogatz, 1998)—mRF neurons are more locally inter-connected, and linked by shorter paths, than networks with the same number connections arranged in random or uniform configurations. This interesting finding implies certain properties, shared by other small-world networks, such as rapid cross-network synchronization and persistent activity, that would be consistent with an action selection role.

How, then, might the mRF operate as an action selection substrate? Humphries et al. (in press) have proposed that activity in individual clusters may represent *sub-actions*—component parts of a coherent behavior. Thus the expression of a behavior should involve the simultaneous activation of clusters representing compatible sub-actions and inhibition of clusters representing incompatible ones. Simulation of model mRF circuits indicates that the pattern of connectivity described above—between cluster excitation and within cluster inhibition—does have the potential to implement such a mechanism (Humphries et al., in press). If this proves to be an appropriate model of the mRF it also suggests that there is a brainstem substrate for action selection that is quite different from either the bank of centralized disinhibitory switches identified in the basal ganglia, or the notion of distributed switching circuits utilizing RI. Future modeling work will hopefully tease out what advantages and disadvantages this novel form of action selection mechanism may convey.

Both the basal ganglia and the reticular formation lie in central positions along the vertebrate main neuraxis (see figure 5), and have been described collectively as forming the brain's 'centrencephalic core'—identified by a number of neurobiologists as playing a key role in the integration of behavior (see Prescott et al., 1999 for review). The mRF is a major target of basal ganglia output via a pathway involving the pedunculopontine nucleus and, in the intact adult brain, it is likely that both systems co-operate to determine what form of behavior is expressed at a given time. The relationship between the two systems may combine aspects of layered (subsumption-like) and hierarchical decomposition of control. Layered, since developmental and decerebrate studies suggest that the mRF can operate, to some degree, without modulation from higher brain structures (including the basal ganglia). Hierarchical since, if there is validity in the conjecture that the mRF provides a *sub-action* decomposition of behavior, patterns of innate behavior could then be selected "in toto" by focal disinhibition from the basal ganglia.

5.5 The role of the cortex in action selection

The evolution of mammals saw a substantial increase in the role of the forebrain in action specification and control (Butler & Hodos, 1996) largely supplementing, rather than replacing, the functionality of motor systems lower down the neuraxis. The mammalian brain consequently possesses a complex layered control architecture providing multiple levels of sensorimotor competence (Prescott et al., 1999). Both cortical and sub-cortical motor systems form action selection 'loops' via the basal ganglia (McHaffie, Stanford, Stein, Coizet, & Redgrave, 2005) providing the option to choose between brainstem systems that provide a rapid response to immediate contingencies, and cortical systems that provide more sophisticated adjudication between alternatives, taking greater account of context, past experiences, and future opportunities. Experiments with mammals, such as rats and cats, in which the cerebral cortex has been completely removed (see Gallistel, 1980; Wishaw, 1990), show that such radical surgery leaves intact the capacity to generate motivated, and integrated behavioral sequences. Decorticate animals lack skilled motor control, are impaired in various learning tasks, and appear more stimulus-bound than control animals, yet they still eat, drink, and groom under appropriate motivational and stimulus conditions, and display many aspects of normal social and sexual behavior. To this extent then, the cortex does not appear to be a critical locus for behavioral integration at least with respect to these animals' basic repertoire of species-typical acts. The mammalian prefrontal cortex, which has long been identified with a general role in 'executive function' (see e.g. Miller & Cohen, 2001), forms similar closed-loop circuits with the basal ganglia to motor cortical areas more directly associated with the control of movement (Hazy, Frank, & O'Reilly, In press). This finding, suggests that the basal ganglia selection mechanisms have been appropriated for use in more cognitive tasks involving, for example, planning, or the selection and maintenance of working memory representations. Areas of prefrontal cortex also act to process reward information, to predict expected outcomes, to monitor performance and catch errors, to evalute cost/benefit trade-offs, and to analyse context (Krawczyk, 2002; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Rushworth et al., 2005; Schall, Stuphorn, & Brown, 2002). In other words, whilst the action selection machinery may be primarily sub-cortical, the cortex provides a much enriched capacity to ensure that the most appropriate actions are selected.

Intrinsic competitive mechanisms within specific cortical areas (Fransen & Lansner, 1998), and forward and back projections between different cortical domains (Duncan, Humphreys, & Ward, 1997; Renart, Parga, & Rolls, 1999), may also contribute to the preference of some courses of action over others. For instance, it is likely that cortical systems have an attractor dynamics that limits the number of alternative courses of action that are available at a given moment (Cisek, in press; Lukashin, Amirikian, Mozhaev, Wilcox, & Georgopoulos, 1996; Weber, Wermter, & Elshaw, 2006). Similarly, selective attention, arising as the result of distributed competitive processes, may help to narrow the range of options available (Deco & Rolls, 2005; Duncan, Humphreys, & Ward, 1997). How these emergent selection processes interact with the more specialized selection circuits in substrates such as the basal ganglia remains to be fully understood.

6 Conclusions—‘forced moves’ and ‘good tricks’ in the evolution of action selection

I have provided a brief review of the neural substrate of action selection in a small number of living animal groups. The particular animals considered were chosen for their proximity to an evolutionary trajectory leading from the very first nervous systems to those of the vertebrate class to which we ourselves belong. Of course, this path leaves out the vast majority of living animals including all the advanced protostome invertebrate classes, such as the insects, that have provided valuable inspiration to recent research in robotics (see e.g. Webb & Consi, 2001). The wider study of the evolutionary neurobiology of both protostome and deuterostome phyla should provide evidence of convergence and divergence in control system design that will help in the search for more evolutionary ‘forced moves’ and ‘good tricks’. The literature on behavioral choice in the nervous systems of simple molluscan and crustacean invertebrates is particularly relevant to this search (for reviews see Davis, 1979; Kovac & Davis, 1980; Kristan & Shaw, 1997; Kupfermann & Weiss, 2001; Elliott & Susswein, 2002; Esch & Kristan, 2002). Neuroethological investigations in such animals have demonstrated several principles consistent with the analysis presented here: (i) that distinct behaviors may involve overlapping neural substrates; (ii) that the control of behavior is often hierarchically organized (such that when the pre-conditions for two or more behaviors are simultaneously met, particular responses are likely to take precedence); (iii) that some neurons (or neuron populations) play specific roles in behavior switching (sometimes characterized as ‘command’ or ‘higher-order’ neurons) (iv) that the activation of motor outputs relevant to one behavior is often accompanied by inhibition of competing outputs; and (v) that selection may often involve di-synaptic inhibitory pathways (i.e. disinhibition). Finally, although the current review has also focused on neural circuits, it is important to note that diffuse regulatory mechanisms, such as the endocrine system[8], can play an important role in action selection (see, e.g. Kandel, Krasne, Strumwasser, & Truman, 1979; Schmitt, 1984; Jung & Scheller, 1991; Kupfermann & Weiss, 2001).

Despite the limitations noted above, I believe that a number of conclusions can be drawn from the findings surveyed.

---

[8] It is interesting to note in this regard, that the first nerve cells may have been neurosecretory, in other words, diffuse chemical signaling may have preceded electrical conduction in the evolution of animal control systems (Horridge, 1968; Mackie, 1990).

First, the investigation of cnidarian nervous systems shows that many forms of behavioral integration can be achieved in complex multi-celled animals in the relative absence of centralized nervous system structures. The elegance of these natural solutions is only just beginning to be matched by those developed for distributed robot control systems, indeed, I suspect that the study of cnidarian nervous systems and behavior could provide some 'good tricks' for the design of future 'minimalist' mobile robots.

Second, the review of trace-fossil data, and of the functional architecture of flatworm nervous systems suggests that the evolution of centralized selection mechanisms in the archaic brain may have been a 'forced move' required to maintain behavioral coherence in a bilaterally-organized animal. The value of fusing centralized action selection with distributed, layered, or behavior-based control has been recognized in the design of a number of robot control architectures (Rosenblatt, 1997; Utete, Barshan, & Ayrulu, 1999; Rosenblatt, 2000; Yavuz & Bradshaw, 2002; DeSouza & Kak, 2004). More generally, it seems likely that the design of artificial control systems could benefit from the use of similar centralized conflict resolution systems because of the advantages that this form of modularity can confer (see Prescott et al., 1999; Bryson, 2000).

Finally, my review of the neural substrate of action selection in vertebrates has identified a number of candidate mechanisms that may be instantiated in their neural circuitry. This evidence suggests the existence of multiple substrates for action selection in the vertebrate nervous system. A key proposal, derived from neurobiological evidence but backed-up by theoretical results from computational models, is that vertebrates exploit specialized selection circuitry found in groups of centralized brain structures—the medial core of the reticular formation and the basal ganglia. It seems possible that the connectional economy of this centralized design, which can act to resolve competitions between functional sub-systems distributed widely in the brain, may be one the reasons that the vertebrate nervous system has scaled successfully with the evolution of animals of larger brain and body size. The design of control systems for robots with multiple actuator sub-systems should benefit from a better understanding of how these different elements of the vertebrate nervous system co-operate to maintain behavioral coherence.

Acknowledgements

The author would like to acknowledge funding from the EPSRC (grant no. EP/C516303/1), and from the EU Framework 6 ICEA project (IST-027819-IP), and to thank Mark Humphries, Jon Chambers, Kevin Gurney, Peter Redgrave, and Joanna Bryson for discussion of some of the topics considered here. This review originated, in part, as a result of a workshop entitled "Towards the Whole Iguana" held in Lanzarote in June 2000. The author is indebted to the organizers of that meeting, David McFarland and Owen Holland, and to its attendees, in particular, Daniel Dennett who read and commented on an earlier version of the manuscript.

References

Adoutte, A., Balavoine, G., Lartillot, N., Lespinet, O., Prud'homme, B., & de Rosa, R. (2000). The new animal phylogeny: Reliability and implications. *Proceedings Of The National Academy Of Sciences Of The United States Of America, 97*(9), 4453-4456.

Albert, J. (1999). Computational modeling of an early evolutionary stage of the nervous system. *Biosystems, 54*(1-2), 77-90.

Baguna, J., & Riutort, M. (2004). Molecular phylogeny of the Platyhelminthes. *Canadian Journal Of Zoology-Revue Canadienne De Zoologie, 82*(2), 168-193.

Baguna, J., Ruiz-Trillo, I., Paps, J., Loukota, M., Ribera, C., Jondelius, U., et al. (2001). The first bilaterian organisms: simple or complex? New molecular evidence. *International Journal Of Developmental Biology, 45*, S133-S134.

Balavoine, G., de Rosa, R., & Adoutte, A. (2002). Hox clusters and bilaterian phylogeny. *Molecular Phylogenetics And Evolution, 24*(3), 366-373.

Barrington, E. J. W. (1967). *Invertebrate structure and function*. Sunbury-on-Thames, UK: Nelson.

Berntson, G. G., & Micco, D. J. (1976). Organization of brainstem behavioral systems. *Brain Research Bulletin, 1*, 471-483.

Berridge, K. C. (1994). The development of action patterns. In J. A. Hogan & J. J. Bolhuis (Eds.), *Causal Mechanisms of Behavioural Development*. Cambridge, UK: CUP.

Brooks, R. A. (1986). A robust layered control system for a mobile robot. *IEEE Journal on Robotics and Automation, RA-2*, 14-23.

Brooks, R. A. (1991). New approaches to robotics. *Science, 253*, 1227-1232.

Brooks, R. A. (1994). *Coherent behaviour from many adaptive processes.* Paper presented at the From Animals to Animats 3: Proceedings of the Third International Conference on the Simulation of Adaptive Behaviour, Brighton, UK.

Bryson, J. (2000). Cross-paradigm analysis of autonomous agent architecture. *Journal of Experimental and Theoretical Artificial Intelligence, 12*(2), 165-189.

Butler, A. B., & Hodos, W. (1996). *Comparative Vertebrate Neuroanatomy*. New York: Wiley-Liss.

Chevalier, G., & Deniau, J. M. (1990). Disinhibition as a basic process in the expression of striatal functions. *Trends in Neurosciences, 13*(7), 277-280.

Cisek, P. (In press). Cortical mechanisms of action selection: The affordance competition hypothesis. *Philosophical Transactions of the Royal Society B. Biological Sciences.*

Crimes, T. P. (1992). Changes in the trace fossil biota across the proterozoic phanerozoic boundary. *Journal Of the Geological Society, 149*(Pt4), 637-646.

Crimes, T. P., & Anderson, M. M. (1985). Trace fossils from late Precambrian—early Cambrian strata of southeastern Newfoundland (Canada): Temporal and environmental implications. *Journal of Paleontology, 59*(2), 310–343.

Davis, W. J. (1979). Behavioral Hierarchies. *Trends in Neurosciences, 2*(1), 5-7.

Deco, G., & Rolls, E. T. (2005). Attention, short-term memory, and action selection: a unifying theory. *Progress in Neurobiology, 76*(4), 236-256.

Dennett, D. (1995). *Darwin's Dangerous Idea*. London: Penguin Books.

DeSouza, G. N., & Kak, A. C. (2004). A subsumptive, hierarchical, and distributed vision-based architecture for smart robotics. *Ieee Transactions On Systems Man And Cybernetics Part B-Cybernetics, 34*(5), 1988-2002.

Duncan, J., Humphreys, G., & Ward, R. (1997). Competitive brain activity in visual attention. *Current Opinion in Neurobiology, 7*(2), 255-261.

Eaton, R. C., Hofve, J. C., & Fetcho, J. R. (1995). Beating the competition - the reliability hypothesis for mauthner axon size. *Brain Behavior and Evolution, 45*(4), 183-194.

Eaton, R. C., Lee, R. K. K., & Foreman, M. B. (2001). The Mauthner cell and other identified neurons of the brainstem escape network of fish. *Progress In Neurobiology, 63*(4), 467-485.

Elliott, C. J. H., & Susswein, A. J. (2002). Comparative neuroethology of feeding control in molluscs. *Journal of Experimental Biology, 205*(7), 877-896.

Erwin, D. H., & Davidson, E. H. (2002). The last common bilaterian ancestor. *Development, 129*(13), 3021-3032.

Esch, T., & Kristan, W. B. (2002). Decision-making in the leech nervous systern. *Integrative And Comparative Biology, 42*(4), 716-724.

Finlay, B. L., & Darlington, R. B. (1995). Linked regularities in the development and evolution of mammalian brains. *Science, 268*, 1578-1584.

Fransen, E., & Lansner, A. (1998). A model of cortical associative memory based on a horizontal network of connected columns. *Network, 9*(2), 235-264.

Gabor Miklos, G. L., Campbell, K. S. W., & Kankel, D. R. (1994). The rapid emergence of bio-electronic novelty, neuronal architectures, and organismal performance. In R. J. Greenspan (Ed.), *Flexibility and Constraint in Behavioural systems*: John Wiley and Sons.

Gallistel, C. R. (1980). *The Organization of Action: a New Synthesis*. Hillsdale, NJ: Lawrence Erlbaum.

Grillner, S., Hellgren, J., Menard, A., Saitoh, K., & Wikstrom, M. A. (2005). Mechanisms for selection of basic motor programs--roles for the striatum and pallidum. *Trends Neurosci, 28*(7), 364-370.

Grimmelikhuijzen, C. J. P., & Westfall, L. A. (1995). The nervous systems of Cnidarians. In O. Breidbach & W. Kutsch (Eds.), *The Nervous Systems of Invertebrates An Evolutionary and Comparative Approach* (pp. 7-24). Basel, Switzerland: Birkhauser Verlag.

Groenewegen, H. J., Wright, C. I., & Beijer, A. V. J. (1996). The nucleus accumbens: Gateway for limbic structures to reach the motor system? *Progress In Brain Research, 107*, 485-511.

Gruber, S. A., & Ewer, D., W. (1962). Observations on the myo-neural physiology of the polyclad. *Planocera gilchristi. Journal of Experimental BIology, **39***, 459-477.

Gurney, K., Prescott, T. J., Wickens, J., & Redgrave, P. (2004). Computational models of the basal ganglia: from membranes to robots. *Trends in Neurosciences, 27*, 453-459.

Halstead, L. B. (1965). Pssammosteiformes (Agnatha): a review with descriptions of new material from the lower Devonian of Poland. I. General part. *Paleontol. Pol.*(13).

Hamner, W. M. (1995). Sensory ecology of scyphomedusae. *Marine and Freshwater Behaviour and Physiology, 26*(2-4), 101-118.

Hazy, T. E., Frank, M. J., & O'Reilly, R. C. (in press). Toward an executive without a homunculus: Computational models of the prefrontal cortex/basal ganglia system. *Philosophical Transactions of the Royal Society B. Biological Sciences.*

Hodos, W. (1982). Some perspectives on the evolution of intelligence and the brain. In D. R. Griffin (Ed.), *Animal Mind—Human Mind*. Berlin: Springer-Verlag.

Horridge, A. (1956). The nervous system of the ephyra larva of *Aurellia aurita*. *Quarterly Journal of Microscopical Science, 97*, 59-74.

Horridge, G. A. (1968). The origins of the nervous system. In G. H. Bourne (Ed.), *The Structure and Function of Nervous Tissue* (Vol. 1, pp. 1-31). New York: Academic Press.

Humphries, M. D., Gurney, K., & Prescott, T. J. (2005). The brainstem reticular formation is a small world, not scale-free network. *Proceedings of the Royal Society B. Biological Science, 273*, 503-531.

Humphries, M. H., Gurney, K., & Prescott, T. J. (In Press). Is there a brainstem substrate for action selection? *Philosophical Transactions Of The Royal Society Of London Series B-Biological Sciences*.

Josephson, R. K. (1974). Cnidarian neurobiology. In L. Muscatine & H. M. Lenhoff (Eds.), *Coelenterate biology: reviews and new perspectives* (pp. 245-273). New York: Academic Press.

Josephson, R. K., & Mackie, G. O. (1965). Multiple pacemakers and the behaviour of the hydroid *Tubularia*. *Journal of Experimental Biology, 43*, 293-332.

Jung, L. J., & Scheller, R. H. (1991). Peptide processing and targeting in the neuronal secretory pathway. *Science, 251*(4999), 1330-1335.

Kandel, E. R., Krasne, F. B., Strumwasser, F., & Truman, J. W. (1979). Cellular mechanisms in the selection and modulation of behavior. *Neurosciences Research Program Bulletin, 17*(4), 529-710.

Knoll, A. H., & Carroll, S. B. (1999). Early animal evolution: Emerging views from comparative biology and geology. *Science, 284*(5423), 2129-2137.

Koopowitz, H. (1970). Feeding behaviour and the role of the brain in the polyclad flatworm, *Planocera gilchristi*. *Animal Behaviour, 1970*(18), 31-35.

Koopowitz, H. (1986). On the evolution of central nervous systems - implications from polyclad turbellarian neurobiology. *Hydrobiologia, 132*, 79-87.

Koopowitz, H. (1989). Polyclad neurobiology and the evolution of central nervous systems. In P. A. V. Anderson (Ed.), *Evolution of the first nervous systems* (pp. 315-327). New York: Plenum Press.

Koopowitz, H., & Keenan, L. (1982). The primitive brains of platyhelminthes. *Trends in Neurosciences, 5*(3), 77-79.

Koopowitz, H., Silver, D., & Rose, G. (1975). Neuronal plasticity and recovery of function in a polyclad flatworm. *Nature, 256*, 737-738.

Koopowitz, H., Silver, D., & Rose, G. (1976). Primitive nervous systems, control and recovery of feeding behavior in the polyclad flatworm, *Notoplana acticola*. *Biological Bulletin, 150*, 411-425.

Kovac, M. P., & Davis, W. J. (1980). Neural mechanisms underlying behavioral choice in pleurobranchaea. *Journal of Neurophysiology, 43*(2), 469-487.

Krawczyk, D. C. (2002). Contributions of the prefrontal cortex to the neural basis of human decision making. *Neuroscience and Biobehavioral Reviews, 26*(6), 631-664.

Kristan, W. B., & Shaw, B. K. (1997). Population coding and behavioral choice. *Current Opinion In Neurobiology, 7*(6), 826-831.

Kupfermann, I., & Weiss, K. R. (2001). Motor program selections in simple model systems. *Current Opinion In Neurobiology, 11*(6), 673-677.

Lacalli, T. C. (1996). Frontal eye circuitry, rostral sensory pathways and brain organization in amphioxus larvae - evidence from 3d reconstructions. *Philosophical Transactions Of the Royal Society Of London Series B- Biological Sciences, 351*(1337), 243-263.

Lingenhohl, K., & Friauf, E. (1994). Giant-neurons in the rat reticular-formation - a sensorimotor interface in the elementary acoustic startle circuit. *Journal Of Neuroscience, 14*(3 Pt1), 1176-1194.

Lovick, T. A. (1972). The behavioral repertoire of precollicular decerebrate rats. *Journal of Physiology, 226*, 4P-6P.

Lukashin, A. V., Amirikian, B. R., Mozhaev, V. L., Wilcox, G. L., & Georgopoulos, A. P. (1996). Modeling motor cortical operations by an attractor network of stochastic neurons. *Biological Cybernetics, 74*(3), 255-261.

Mackie, G. O. (1990). The elementary nervous-system revisited. *American Zoologist, 30*(4), 907-920.

Mackie, G. O. (2004a). Central neural circuitry in the jellyfish Aglantha: a model 'simple nervous system'. *Neurosignals, 13*(1-2), 5-19.

Mackie, G. O. (2004b). Epithelial conduction: recent findings, old questions, and where do we go from here? *Hydrobiologia, 530-31*, 73-80.

Mackie, G. O., & Meech, R. W. (2000). Central neural circuitry in the jellyfish Aglantha Digitale III. The rootlet and pacemaker systems. *The Journal of Experimental Biology, 203*, 1797-1807.

Maes, P. (1995). Modelling adaptive autonomous agents. In C. G. Langton (Ed.), *Artificial Life: An Overview*. Cambridge, MA: MIT Press.

Mallatt, J., & Chen, J. Y. (2003). Fossil sister group of craniates: Predicted and found. *Journal Of Morphology, 258*(1), 1-31.

Mataric, M. J. (1990). *A Distributed Model for Mobile Robot Environment-Learning and Navigation* (Masters thesis No. AITR-1228). Cambridge, Mass.: MIT AI Lab.

Mataric, M. J. (1997). Behavior-based control: examples from navigation, learning, and group behavior. *Experimental and Theoretical Artificial Intelligence, 9*(2-3), 323-336.

McFarland, D. (1971). *Feedback Mechanisms in Animal Behaviour*. London: Academic Press.

McFarland, D. (1989). *Problems of Animal Behaviour*. Harlow, UK: Longman.

McHaffie, J. G., Stanford, T. R., Stein, B. E., Coizet, V., & Redgrave, P. (2005). Subcortical loops through the basal ganglia. *Trends in Neurosciences, 28*(8), 401-407.

Medina, L., & Reiner, A. (1995). Neurotransmitter organization and connectivity of the basal ganglia in vertebrates - implications for the evolution of basal ganglia. *Brain Behavior and Evolution, 46*(4-5), 235-258.

Meech, R. W. (1989). The electrophysiology of swimming in the jellyfish Aglantha digitale. In P. A. V. Anderson (Ed.), *Evolution of the first nervous systems*. New York: Plenum Press.

Meech, R. W., & Mackie, G. O. (2001). Two escape swim synaptic inputs in the jellyfish *Aglantha digitale*. *Journal Of Physiology-London, 536*, 132P-132P.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24*, 167-202.

Mink, J. W., & Thach, W. T. (1993). Basal ganglia intrinsic circuits and their role in behavior. *Current Opinion In Neurobiology, 3*, 950-957.

Montes González, F., Prescott, T. J., Gurney, K., Humphries, M., & Redgrave, P. (2000). An embodied model of action selection mechanisms in the vertebrate brain. In J. A. Meyer (Ed.), *From Animals to Animats 6: Proceedings of the 6th International Conference on the Simulation of Adaptive Behavior* (pp. 157-166). Cambridge, MA: MIT Press.

Nilsson, D. E., Gislen, L., Coates, M. M., Skogh, C., & Garm, A. (2005). Advanced optics in a jellyfish eye. *Nature, 435*(7039), 201-205.

Northcutt, R. G. (1994). An immunohistochemical study of the telencephalon and the diencephalon in a myxinoid jawless fish, the pacific hagfish, *Eptatretus stouti*. *Brain, Behavior, and Evolution, 43*, 140-161.

Northcutt, R. G. (1996). The agnathan ark - the origin of craniate brains. *Brain Behavior and Evolution, 48*(5), 237-247.

Northcutt, R. G. (2002). Understanding vertebrate brain evolution. *Integrative And Comparative Biology, 42*(4), 743-756.

Northcutt, R. G. (2005). The new head hypothesis revisited. *Journal Of Experimental Zoology Part B-Molecular And Developmental Evolution, 304B*(4), 274-297.

Prescott, T. J., Bryson, J. J., & Seth, A. (In Press). Modelling natural action selection: an introduction to the theme issue. *Philosophical Transactions of the Royal Society. B. Biological Sciences.*

Prescott, T. J., Montes González, F., Humphries, M. D., Gurney, K., & Redgrave, P. (2006). A robot model of the basal ganglia: Behaviour and intrinsic processing. *Neural Networks, 19*(1), 31-61.

Prescott, T. J., Gurney, K., & Redgrave, P. (2002). Basal Ganglia. In M. A. Arbib (Ed.), *The Handbook of Brain Theory and Neural Networks* (2nd ed., pp. 147–151). Cambridge, MA: MIT Press.

Prescott, T. J., & Ibbotson, C. (1997). A robot trace-maker: Modeling the fossil evidence of early invertebrate behavior. *Artificial Life, 3(4)*, 289-306.

Prescott, T. J., Redgrave, P., & Gurney, K. N. (1999). Layered control architectures in robots and vertebrates. *Adaptive Behavior, 7*(1), 99-127.

Raikova, O. I., Reuter, M., Gustafsson, M. K. S., Maule, A. G., Halton, D. W., & Jondelius, U. (2004). Evolution of the nervous system in *Paraphanostoma* (Acoela). *Zoologica Scripta, 33*(1), 71-88.

Raup, D. M., & Seilacher, A. (1969). Fossil foraging behaviour: computer simulation. *Science, 166*, 994-995.

Redgrave, P., Prescott, T., & Gurney, K. N. (1999). The basal ganglia: A vertebrate solution to the selection problem? *Neuroscience, 89*, 1009-1023.

Renart, A., Parga, N., & Rolls, E. T. (1999). Backward projections in the cerebral cortex: implications for memory storage. *Neural Computation, 11*(6), 1349-1388.

Reuter, M. (1989). From innovation to integration: Trends of the integrative systems in microturbellerians. In M. K. S. Gustafsson & M. Reuter (Eds.), *The Early Brain: Proceedings of the Syposium "Invertebrate Neurobiology"* (pp. 161-178). Abo, Finland, Abo Academy Press.

Reuter, M., & Gustafsson, M. K. S. (1995). The flatworm nervous system: Pattern and phylogeny. In O. Breidbach & W. Kutsch (Eds.), *The Nervous Systems of Invertebrates An Evolutionary and Comparative Approach* (pp. 25-59). Basel, Switzerland: Birkhauser Verlag.

Ridderinkhof, K. R., van den Wildenberg, W. P., Segalowitz, S. J., & Carter, C. S. (2004). Neurocognitive mechanisms of cognitive control: the role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain and Cognition, 56*(2), 129-140.

Ringo, J. L. (1991). Neuronal interconnection as a function of brain size. *Brain, Behaviour, and Evolution, 38*, 1-6.

Romanes, G. J. (1885). *Jellyfish, Starfish, and Sea Urchins, Being a Research on Primitive Nervous Systems*. New York: D. Appleton.

Rosenblatt, J. K. (1997). DAMN: A distributed architecture for mobile navigation. *Journal Of Experimental & Theoretical Artificial Intelligence, 9*(2-3), 339-360.

Rosenblatt, J. K. (2000). Optimal selection of uncertain actions by maximizing expected utility. *Autonomous Robots, 9*(1), 17-25.

Ruiz-Trillo, I., Riutort, M., Fourcade, H. M., Baguna, J., & Boore, J. L. (2004). Mitochondrial genome data support the basal position of Acoelomorpha and the polyphyly of the Platyhelminthes. *Molecular Phylogenetics And Evolution, 33*(2), 321-332.

Ruiz-Trillo, I., Riutort, M., Littlewood, D. T. J., Herniou, E. A., & Baguna, J. (1999). Acoel flatworms: Earliest extant bilaterian metazoans, not members of platyhelminthes. *Science, 283*, 1919-1923.

Rushworth, M. F., Buckley, M. J., Gough, P. M., Alexander, I. H., Kyriazis, D., McDonald, K. R., et al. (2005). Attentional selection and action selection in the ventral and orbital prefrontal cortex. *Journal of Neuroscience, 25*(50), 11628-11636.Saper, C. B., Scammell, T. E., & Lu, J. (2005). Hypothalamic regulation of sleep and circadian rhythms. *Nature, 437*(7063), 1257-1263.

Satterlie, R. A. (2002). Neuronal control of swimming in jellyfish: a comparative story. *Canadian Journal Of Zoology, 80*(10), 1654-1669.

Satterlie, R. A., & Nolen, T. G. (2001). Why do cubomedusae have only four swim pacemakers? *Journal of Experimental Biology, 204*(8), 1413-1419.

Schall, J. D., Stuphorn, V., & Brown, J. W. (2002). Monitoring and control of action by the frontal lobes. *Neuron, 36*(2), 309-322.

Scheibel, A. B. (1984). The brainstem reticular core and sensory function. In J. Brookhart, M. & V. B. Mountcastle (Eds.), *Handbook of Physiology, Section 1: The Nervous System* (pp. 213-256). Bethesda, Maryland: American Physiological Society.

Scheibel, M. E., & Scheibel, A. B. (1967). Anatomical basis of attention mechanisms in verterbrate brains. In G. C. Quarton, M. T. & F. O. Schmitt (Eds.), *The Neurosciences: A Study Program* (pp. 577-602). New York: Rockefeller University Press.

Schmitt, F. O. (1984). Molecular regulators of brain-function - a new view. *Neuroscience, 13*(4), 991-1001.

Shu, D.-G., Luo, H.-L., & Conway Morris, S. (1999). Lower Cambrain vertebrates from south China. *Nature,* ***402***, 42-46.

Snaith, S., & Holland, O. (1990). An investigation of two mediation strategies suitable for behavioural control in animals and animats. Paper presented at *From Animals to Animats: Proceedings of the First International Conference Simulation of Adaptive Behaviour*, Paris.

Spencer, A. N., Przysiezniak, J., & Acosta-Urquidi, J. (1989). Presynaptic spike-broadening reduces junctional potential amplitude. *Nature, 340*, 636-638.

Utete, S. W., Barshan, B., & Ayrulu, B. (1999). Voting as validation in robot programming. *International Journal Of Robotics Research, 18*(4), 401-413.

Valentine, J. W. (1994). Late precambrian bilaterians - grades and clades. *Proceedings Of The National Academy Of Sciences Of The United States Of America, 91*(15), 6751-6757.

Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. *Nature, 393*, 440-442.

Webb, B., & Consi, T. R. (2001). *Biorobotics*. Cambridge, MA: MIT Press.

Weber, C., Wermter, S., & Elshaw, M. (2006). A hybrid generative and predictive model of the motor cortex. *Neural Networks, 19*(4), 339-353.

Windhorst, U. (1996). On the role of recurrent inhibitory feedback in motor control. *Progress In Neurobiology, 49*(6), 517-587.

Wishaw, I. Q. (1990). The decorticate rat. In B. Kolb & R. C. Tees (Eds.), *The Cerebral Cortex of the Rat* (pp. 239-267). Cambridge, MA: MIT Press.

Woods, J. W. (1964). Behavior in chronic decerebrate rats. *Journal of Neurophysiology, 27*(645-644).

Yavuz, H., & Bradshaw, A. (2002). A new conceptual approach to the design of hybrid control architecture for autonomous mobile robots. *Journal Of Intelligent & Robotic Systems, 34*(1), 1-26.